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PRIMARY RESEARCH PAPER

Towards a more precisely defined macrophyte-dominated regime: the recent history of a shallow lake in Eastern Poland

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Abstract Archived data and sedimentary macrofossil records of vegetation and invertebrates deposited in a 60-cm long sediment core were analysed to examine if macrophyte dominance was a permanent feature of the recent history of lowland Lake Kleszczów. For the last several centuries, the lake has not been dominated by phytoplankton but by floating-leaved vegetation at strongly reduced water level. Starting from the mid-nineteenth century, probably as a result of climate fluctuations, vegetation switched at first into submerged angiosperms, and then, in the second half of twentieth century, towards charophytes. Within charophytes there were switches between *Chara globularis* and *C. vulgaris* communities, depending on lake productivity or hydrological stress. No symptoms were detected of a switch to a turbid regime as a result of potential internal supply of phosphorus from sediments covered with a dense carpet of charophytes. Our study shows that within a longer period with clear water, the community of macro-vegetation can be highly dynamic. It can be represented by various types of vegetation as a response to different productivity levels and/or hydrological stress, largely determining the composition of other hydrobionts and course of various processes, and as a consequence, the functioning of the ecosystem and its resilience.

Keywords Submerged angiosperms · Charophytes · Invertebrates · Alternative states · Eutrophication · Hydrological stress · Clear water phase

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Introduction

The first papers concerning the relationships between macrophytes and phytoplankton in determining lake water transparency appeared in the 1980s (Timms & Moss, 1984; Carpenter & Lodge, 1986). Their crucial significance in the unravelling of the functioning of lakes was emphasised by the formulation of the theory of alternative stable states (Scheffer et al., 1993;

Scheffer & Jeppesen, 1998; Moss, 2007b). Since the appearance of the alternative stable state concept, global research on various aspects of the functioning of shallow lakes has intensified, especially because knowledge of the subject was of key importance for lake management and restoration measures (Moss et al., 1996; Jeppesen, 1998; Scheffer, 1998; Jeppesen et al., 2007; Moss, 2007b). As a result, the concept of alternative stable states has developed, and the perception of the state generally described as macrophyte-dominated has been specified in more detail, showing that the state can be represented by the dominance of among others free-floating plants, charophytes, or submerged angiosperms (Blindow et al., 1993; Scheffer & van Nes, 2007; Blindow et al., 2014).

Transitional states between macrophyte-dominated and phytoplankton-dominated systems have been observed (Scheffer & Jeppesen, 1998, 2007). Such states are thought to be considerably less stable and more often shift to the turbid water state. These transitional stages can have a relatively short duration in the case of strong disturbances (Scheffer et al., 1993; Scheffer & Jeppesen, 1998), or a relatively long duration, if increased supply of nutrients results in gradual replacement of macrophytes with planktonic algae (Jones & Sayer, 2003; Sayer et al., 2010a; Hilt et al., 2013).

It has been shown in several European lakes that the macrophyte-dominated state can cyclically shift into the phytoplankton-dominated state and back every several years with no evident external stimuli (Rip et al., 2005; Van Geest et al., 2005; Hargeby et al., 2007; van Nes et al., 2007). A similar phenomenon was observed in Boreal lakes of northern Canada (Bayley et al., 2007).

The determination of the current state of a lake is not problematic if data are available. However, it becomes a challenge when attempting to determine the lake regime in the distant past. Monitoring data from such periods are usually scarce or non-existent, with some exceptions (Egertson et al., 2004; Hargeby et al., 2007; Sand-Jensen et al., 2008; Hilt et al., 2013; Hobbs et al., 2014). In situation without reliable long-term monitoring data, studies into historical ecosystem state can be supported by paleolimnological analyses (Battarbee et al., 2005; Sayer et al., 2010a; Madgwick et al., 2011; Kowalewski et al., 2013, 2015). This particularly concerns shallow lakes distinguished by abundant development of macrophytes accompanied by a rich invertebrate fauna, and providing conditions favourable for the deposition of macrofossils (Rawcliffe et al., 2010).

This paper concerns the history of the shallow Lake Kleszczów, which, according to historical data, has remained in a clear-water macrophyte-dominated state over the last several decades. Based on the archived data, and plant and animal macrofossils contained in the sediments, we hypothesise that the current macrophyte-dominated state of the lake has been a persistent feature over recent centuries. We attempted to determine the stability of the lake regime, and to identify drivers that could affect its dynamics. First a detailed description of the history of the lake is given to document how different regimes existed in different periods of the lake's history. We then discuss these observations in the context of a conceptual framework of alternative stable states in shallow lakes.

Methods

Study site

Lake Kleszczów (51°31′5″N, 22°53′20″E) is located in the River Tyśmienica drainage basin, in the eastern part of Poland in the Łęczna-Włodawa Lakeland, a part of a larger physio-geographical region called Lublin Polesie, occupying a plain of low relief (<30 m). The lake's basin, with an area of 45 ha is flat, and depth does not exceed 2 m over most of its area. Currently, the observed maximum depth oscillates around 3 m. The lake is groundwater fed, and has one periodically functioning outflow to the Bobrówka River. The lake's eastern and northern shore is adjacent to a pine forest. The remainder borders on the floating mat formed by a transitional mire located in the southern part of the lake-peatland complex, and a fen adjacent to the lake to the north-west.

The catchment of the lake has an area of 253.4 ha. It is occupied by arable land (45%), forests and coppices (32%), and grasslands (23%). The relatively small lake area, compared with the lake's terrestrial catchment, the infertile sandy soils in the drainage area (mostly brown and rusty soils), and low atmospheric nutrient load suggest only a small influence of external factors on the in-lake processes (Smal et al., 2005).

The climate of the area is continental with the mean temperature of the coldest month (January) reaching −4°C. Precipitation in the region is quite low (560 mm per year), with relatively high evapotranspiration (450 mm), often exceeding precipitation during spring and summer (Wilgat et al., 1997).

Historical lake surveys

Lake Kleszczów has been the subject of several short-term research projects since the early 1950s. The longest series of surveys concerns macrophytes. The observations come from 1953 to 1958 (Fijałkowski, 1959), 1968–1969 (Popiołek, 1971), 1995 (Sugier & Czarnecka, 1998), 2000–2007 (Lorens & Sugier, 2001; Kornijów et al., 2002; Lorens & Sugier, 2010). Data included in these papers permitted the contemporary reconstruction of the distribution of the lake's vegetation. This also involved use of monochromatic aerial photographs taken in 1958 and 1983, and colour aerial photographs from 1997, topographic maps at a scale of 1:10,000 (geodetic coordinates 1965) prepared in 1976, and satellite images from Google and Geoportal resources.

Other data sets used in this paper concern water chemistry (Radwan et al., 1971; Kowalczyk, 1979; Smal et al., 2005); reports of the Provincial Inspectorate of Environment Protection in Lublin from 2008, 2010, and 2013, phytoplankton (Kornijów et al., 2002), zooplankton (Kowalczyk, 1979; Adamczuk & Kornijów, 2011), macroinvertebrates (Tarkowska-Kukuryk & Kornijów, 2008), and fish (Kornijów et al., 2002).

Paleolimnological survey: sediment core collection, chronology and macrofossil analysis

A 60 cm long sediment core (51°31′6.4″N, 22°53′21.7″E; depth 270 cm) was taken in June 2013 with a gravity corer (UWITEC, Co., Austria), equipped with a 86-mm inner diameter tube. The bottom was overgrown by a dense *Chara* bed, making sediment sampling complicated. The core was taken after prior location by a diver of about 1 square meter of the bottom free from vegetation. The core was subsampled at 1-cm intervals by means of a sediment slicer (Kornijów, 2013), and stored at 4 °C for subfossil analysis.

The sediment sequence was dated by ^{210}Pb determination combined with ^{137}Cs stratigraphy and radiocarbon dating. The activity of ^{210}Pb and ^{137}Cs were determined by low background high-resolution gamma-spectrometry using a HPGe detector by Canberra. Specific activity of unsupported ^{210}Pb was calculated from total activity by subtraction of ^{226}Ra activity assuming isotopic equilibrium between them. The CRS model of dating was then applied (Appleby, 2001). For one macrofossil from the lower part of the sequence, radiocarbon activity was also measured by means of an AMS spectrometer at the Poznań Radiocarbon Laboratory. The results were calibrated using OxCal software (Bronk Ramsey, 2009) and IntCal13 calibration curve (Reimer et al., 2013). The age-depth model was calculated for the entire sequence by means of MOD-AGE software (Hercman & Pawlak, 2012; Hercman et al., 2014). The model was calculated from age probability distributions using the randomisation method. Normal (Gauss) distribution of ages was assumed for ^{210}Pb dates. For radiocarbon dates, age probability distribution calculated by OxCal was applied. The age-depth function was fitted using the LOESS (locally weighted scatter plot smoothing) procedure. LOESS gives greater weight to data points located closer to the points of estimation than to those located farther away. The SPAN factor, which is defined as the percentage of data points that are used for the model estimation, was 5, which provides the smoothest model consistent with the data.

The entire sample of 40–50 cm^3 (1 cm thickness of the core) every 1 cm in the uppermost 20 cm and every 5 cm below was washed through a 0.125 mm mesh sieve for macrofossils. The residue was examined under a stereo-microscope at 10–100 magnification. Recognisable plant and animal fossils were isolated, identified, and counted. For the smallest fossils, a quantitative sub-sample (5–10 cm^3 of material suspended in water) was examined, and fossils were quantified. All plant and invertebrate fossils, excluding Chironomidae, are expressed in numbers per 100 cm^3 of fresh sediment. The chironomid analysis generally followed Warwick (1980). Subfossil material was sieved through a 0.125 mm screen. A total of ≥50 head capsules were counted in each sample. Head capsules were identified following Wiederholm (1983) and Brooks et al. (2007).

Stratigraphic diagrams were plotted with the application of Tilia version 2 and Tilia-Graph (Grimm, 1992).

Chironomidae were expressed as percentages. The organisms encountered, except macrophytes, were divided into three ecological assemblages: plant-associated, sediment-associated and planktonic, depending on their habitat preferences (Kornijów & Gulati, 1992; Brodersen et al., 2001; Kornijów et al., 2005; Carey et al., 2008; Tarkowska-Kukuryk & Kornijów, 2008; Kornijów et al., 2010; Rybak & Błędzki, 2010; Kornijów et al., 2016). Macrofossils and chironomids were subject to a stratigraphically-constrained cluster analysis in order to determine zones with the application of the CONISS software (Grimm, 1987) included in the Tilia-Graph package (Grimm, 1992). Stratigraphic zones were identified using Orloci's chord distance (Legendre & Legendre, 1998). Taxa were square root transformed to down-weight dominants.

Results

Historical lake surveys

Chemistry

The physical and chemical properties of the lake's water over the last 50 years have been relatively stable, except for water transparency which strongly declined in 1968, and for some fluctuations in TP (Table 1). The lake water showed relatively low electrical conductivity, suggesting low concentration of dissolved mineral substances. The concentrations of nutrients, nitrogen and phosphorus, and chlorophyll *a* were generally low, indicating mesotrophic conditions typical of lakes dominated by macrophytes (Zimmer et al., 2003; Bayley et al., 2007).

Lake biota

In the 1950s macrophytes covered almost the entire lake bottom (Fig. 1). The lake's central region was dominated by *Ceratophyllum demersum* L. (Fijałkowski, 1959). Shallower near-shore parts of the littoral along the northern and eastern shore were inhabited by charophytes, dominated by *Chara globularis* Thuiller, and the southern and western edges by communities with dominance of *Elodea canadensis* Michx. and *Stratiotes aloides* L. The emergent vegetation was dense and dominated by *Phragmites australis* (Cav.) Trin. ex Steud) on the northern and eastern shore, with patches of *Typha angustifolia* L. and *T. latifolia* L. in the southern and western part.

Years 1960–1970 were a period of intensive melioration and hydrotechnical works, and increased hydrological stress. Drainage works conducted in the 1960s converted the adjacent peatlands into meadows and led to a decrease in water level with a maximum depth of 1.3 m, and to major changes in the vegetation,

Table 1 Data set on the water chemistry of Lake Kleszczów over the last 50 years according to various authors

Year of research	Secchi Disc (m)	Chl a (μg l^{-1})	Conduct. (μS cm^{-1})	pH	TN (mg N l^{-1})	TP (μg P l^{-1})	Source
2013	2.1	nd	129	7.85	1.51	37	PIEC (2013)
2010	1.87	4.1	206	nd	1.74	19	PIEC (2010)
2008	2.0	4.1	nd	nd	2.19	21	PIEC (2008)
2006	2.1	5.5	nd	nd	0.96	20	PIEC (2008)
2001	2.95	4.4	117	7.7	0.90	29	Kornijów et al. (2002)
1999	2.1	4.3	119	nd	0.91	40	PIEC (1999)
1995	2.4	nd	98	7.62	nd	nd	Own data
1993	2.0	4.7	94	8.85	1.15	60	PIEC (1994)
1968	1.0	nd	nd	7.5	nd	25	Kowalczyk (1979)
1966	2.24	nd	nd	9.5	nd	nd	Radwan et al. (1971)

PIEC 1994, 2008, 2010, 2013—reports by the Provincial Inspectorate of Environment Control in Lublin, published in particular years. The values are summer means from two measurements, except for 1966 and 1968 when the study was performed once a year

nd no data

with distinct dominance of angiosperms (Fig. 1). Plant communities in the central part of the lake developed as layered patches with a dominant *Stratiotes aloides* in the upper layer, and *Elodea canadensis* and *Ceratophyllum demersum* below (Popiołek, 1971). The shallower parts of the lake were mostly overgrown with *Myriophyllum spicatum* L. A drastically smaller area, in comparison with the mid 1950s was occupied by charophytes, particularly *Chara vulgaris* L., dispersed in the near-shore area. The water level decrease exposed the mineral bottom in the northern and eastern part of the lake, resulting in an expansion of helophytes dominated by *P. australis*, *Schoenoplectus lacustris* (L.) Palla, *Carex rostrata* Stokes, *C. lasiocarpa* Ehrh., *Eleocharis palustris* (L. Roem. & Schult.), and *Equisetum fluviatile* L.

In 1985 the canal sluice joining the lakes Kleszczów and Miejskie was permanently locked (filled with soil), which led to a temporary decline in the lake-level by ~0.7 m. Ten years later, at a water level almost twice as high as compared to the previous period and relatively low natural water level fluctuations, almost the entire central part of the lake was occupied by charophytes with dominance of *C. vulgaris*. Only small patches of angiosperms, dominated by *M. spicatum,* were recorded (Fig. 1). Along the northern, western, and southern shore, nymphaeids developed, including *Nuphar lutea* (L.) Sibth. & Sm., *Nymphaea alba* L. and *N. candida* J. Presl & C. Presl. The floristic diversity of the emergent belt decreased and became dominated by *P. australis*.

Over the last 20 years, the submerged vegetation has been dominated by charophytes, with predominance of *C. globularis* at the turn of twentieth century, and *C. globularis* and *Chara delicatula* Kütz. in 2014. There were slight changes in the area occupied by floating-leaved and emergent vegetation.

In 2000–2001 the density of zooplankton crustaceans was relatively low (156 l^{-1}), and the community was dominated by *Ceriodaphnia quadrangular* (O. F. Müller), with less numerous *Bosmina coregoni* Baird, *Bosmina longirostris* (O. F. Müller), and *Chydorus sphaericus* (O. F. Müller). No *Daphnia* were recorded in the plankton (Adamczuk & Kornijów, 2011). Data on zoobenthos and epiphytic fauna (except for Bryozoa and Porifera) are given in Kornijów et al. (2002) and Tarkowska-Kukuryk & Kornijów (2008). Non-piscivorous fish were dominated by roach *Rutilus rutilus* L. Piscivores, including northern pike *Essox lucius* L. and European perch *Perca fluviatilis* L., constituted 56% of the total fish biomass (Kornijów et al., 2002).

Paleolimnological survey

Sediment core description and dating

The sediments were composed of gyttja. The analysed samples showed very low activity of ^{210}Pb and ^{137}Cs owing to their low density and high organic contents (Fig. 2). Total activity of ^{210}Pb decreased with depth, and was equal to that of supported ^{210}Pb below 20 cm. The calculated age-depth model is realistic for the sediment section 0–40 cm. The radiocarbon date (from 40 cm; Poz-57952, 380 ± 70 BP) was in agreement with the model based only on ^{210}Pb dating. ^{137}Cs stratigraphy suggests that the top 17 cm has been deposited since the late 1950s. The relatively high uncertainly of ^{137}Cs activity measurements masked the caesium bomb-tests peak of the 1960s. The Chernobyl peak was clearly visible and was noted in the horizon at 9 cm (^{210}Pb date AD 1986 ± 3).

Macrofossil stratigraphy

Twelve plant and 21 invertebrates taxa overall were recorded in the sediment layers analysed. Three zones of fossil remains were distinguished based on their distribution in the sediment profile (Figs. 3 and 4).

The lowest zone (60–21 cm) contained abundant remains of floating-leaved *Nymphaea* (Fig. 3). They were accompanied by scarce fossils of *Ceratophyllum* sp. and *Najas marina* L., as well as episodic occurrences of *Nitella* sp., *Chara* sp. and *Myriophyllum* sp. Emergent plants were represented by *Typha* sp. and *Phragmites* sp., suggesting a well-developed emergent zone.

Plant-associated fauna included a high contribution of cocoons of predatory Turbellaria, remains of the bryozoan filter-feeder *Plumatella* sp., and head capsules of the chironomid, *Tanytarsus* spp. (Fig. 4). Their relative numbers, however, gradually decreased in favour of the chironomid *Glyptotendipes* sp., typical of more productive habitats.

Sediment-associated invertebrates in the lower part of the core were dominated by the chironomid *Corynocera ambigua* Zett. Above 40 cm, the percentages of *C. ambigua* rapidly decreased, and from this

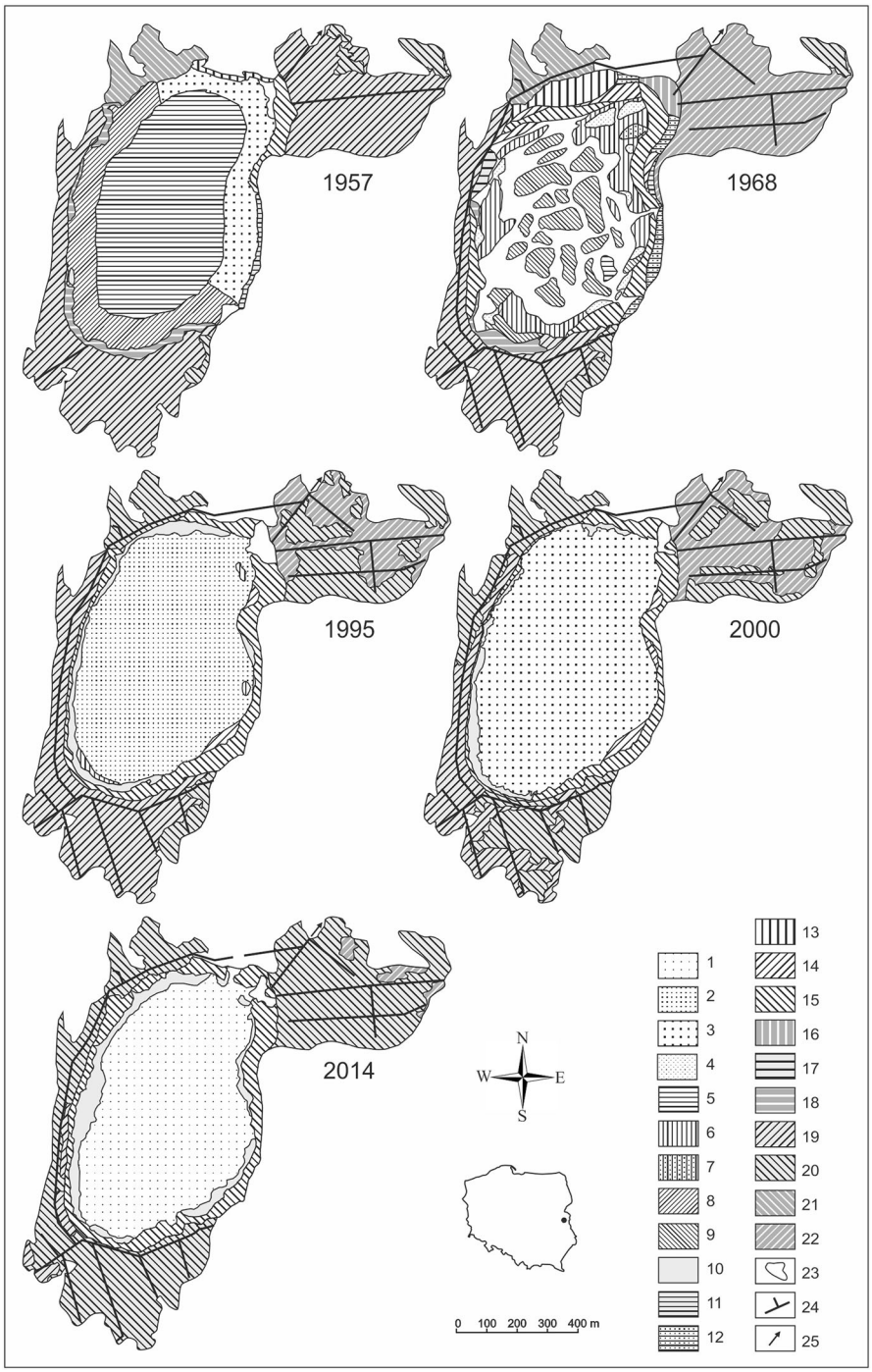

Fig. 1 Changes in the vegetation assemblages in the basin of Lake Kleszczów and adjacent peatlands over the last 60 years; 1—*Chara globularis* and *C. delicatula*, 2—*C. vulgaris* and *C. globularis*, 3—*C. globularis*, 4—*C. vulgaris*, 5—*Ceratophyllum demersum*, 6—*Myriophyllum spicatum*, 7—*Myriophyllum alterniflorum*, 8—*Elodea canadensis*, 9—*Stratiotes aloides*, 10—*Nuphar lutea* and *Nymphaea alba*, 11—*Equisetum fluviatile*, 12—*Carex rostrata*, 13—*Eleocharis palustris,* 14—*Schoenoplectus lacustris*, 15—*Phragmites australis*, 16—*Carex lasiocarpa*, 17—*Sparganium erectum*, 18—*Typha angustifolia*, 19—*Carex lasiocarpa* and *Carex limosa* (transitional mire), 20—*Salix cinerea* and *Betula pubescens* (scrublands), 21—fen dominated by high sedges, 22—meadow, 23—littoral without vegetation, 24—drainage ditch, 25—direction of water outflow. Data sources are Fijałkowski: (1959); Popiołek (1971); Sugier & Czarnecka (1998); Lorens & Sugier (2001); and this study

point on its occurrence was irregular. Other chironomids, such as *Polypedilum* sp., *Einfeldia* sp., and *Microtendipes pedellus* (De Geer), occured throughout the core, showing only slight fluctuations in their percentages. Plankters were most abundantly represented by colony-forming cyanobacteria *Gloeotrichia echinulata* P.G. Richter and ephippia of *Daphnia* sp. The highest numbers of their remains were contained

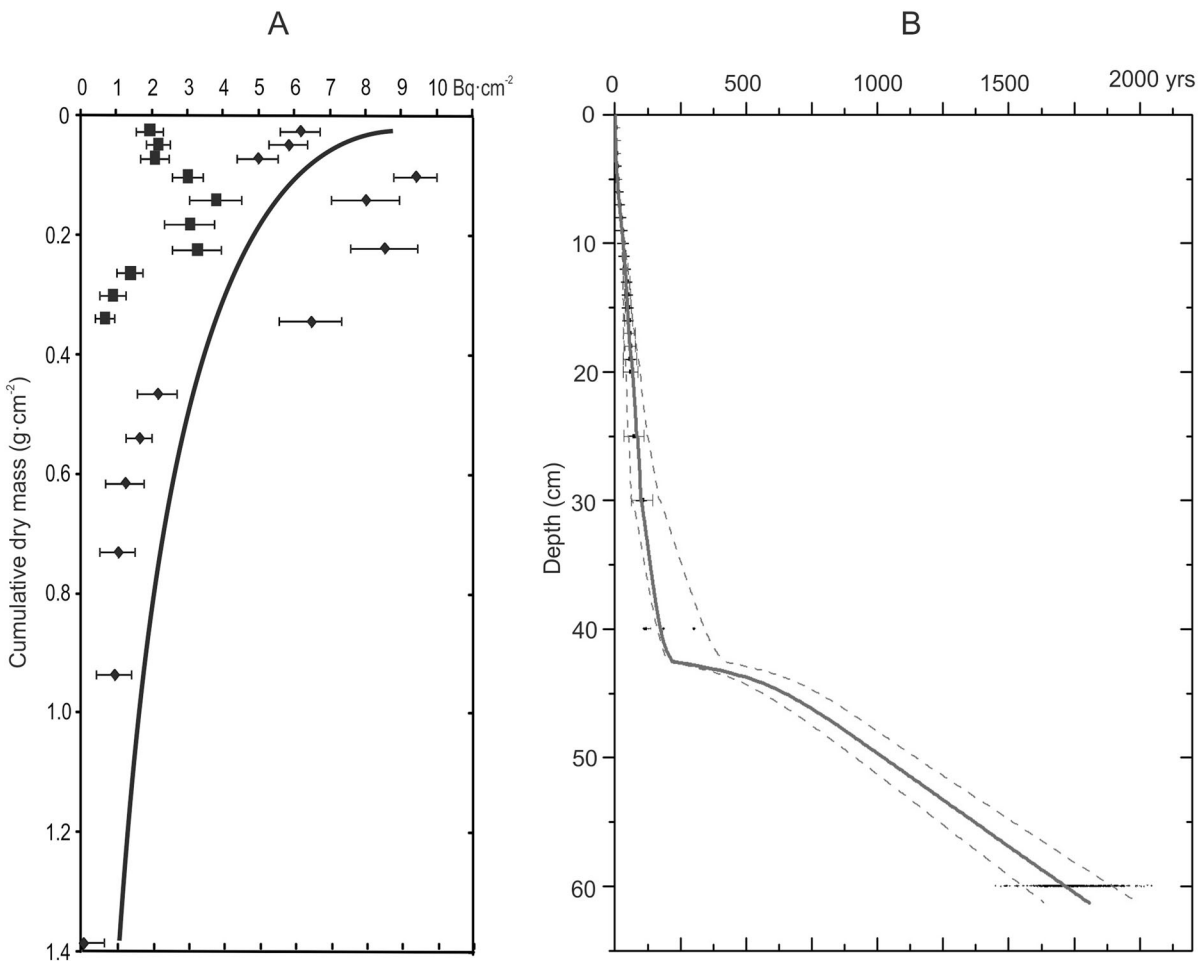

Fig. 2 **A** Activity of unsupported ^{210}Pb (*diamonds*) and ^{137}Cs (*rectangles*), and **B** the age-depth model (*solid line*) and its confidence bands (*dashed lines*) for a sediment core KL-2

in the sediment sections between 50 and 40 cm (Fig. 4).

In zone 2 (20–11 cm), oospores of *Chara* sp. and remains of angiosperms appeared and increased, and the numbers of nymphaeids gradually declined (Fig. 3). *Myriophyllum* sp. remains reached their maximum values. The contribution of plant-associated *Glyptotendipes* sp., Bryozoa, Turbellaria and *Tanytarusus* spp. decreased, while that of *Tanytarsus* spp. increased (Fig. 4). Sediment-associated fauna were represented mostly by *Einfeldia* sp. and the cladoceran *Leydigia* sp., which occurred in small numbers. In the upper part *Einfeldia* sp. had high abundances, which declined slightly near the top of this zone. The opposite pattern to *Einfeldia* was shown by *Chironomus* sp. Numerous remains of phantom-midge (*Chaoborus* sp.) larvae occurred only in the upper part of this zone. Among pelagic organisms, *Gleotrichia* sp. and *Daphnia* sp. maintained a level of density similar to the previous layer (Fig. 4).

In zone 3 (10–1 cm), the dominance of submerged plants was strengthened (Fig. 3). They reached the highest numbers here in the entire core. Nymphaeids were scarce. This zone was abundant in plant-associated fauna, again dominated by Bryozoa, and particularly photophilous *Cristatella mucedo* Cuvier (Fig. 4). High numbers were reached by Turbellaria, cladoceran *Simocephalus* sp., and chironomids: *Dicrotendipes* sp., *Glyptotendipes* sp., *Psectrocladius* sp., and *Tanytarsus* spp. *Piscicola geometra* L., which is a fish ectoparasite, was also abundant. Unlike the plant-associated fauna, the benthic assemblage

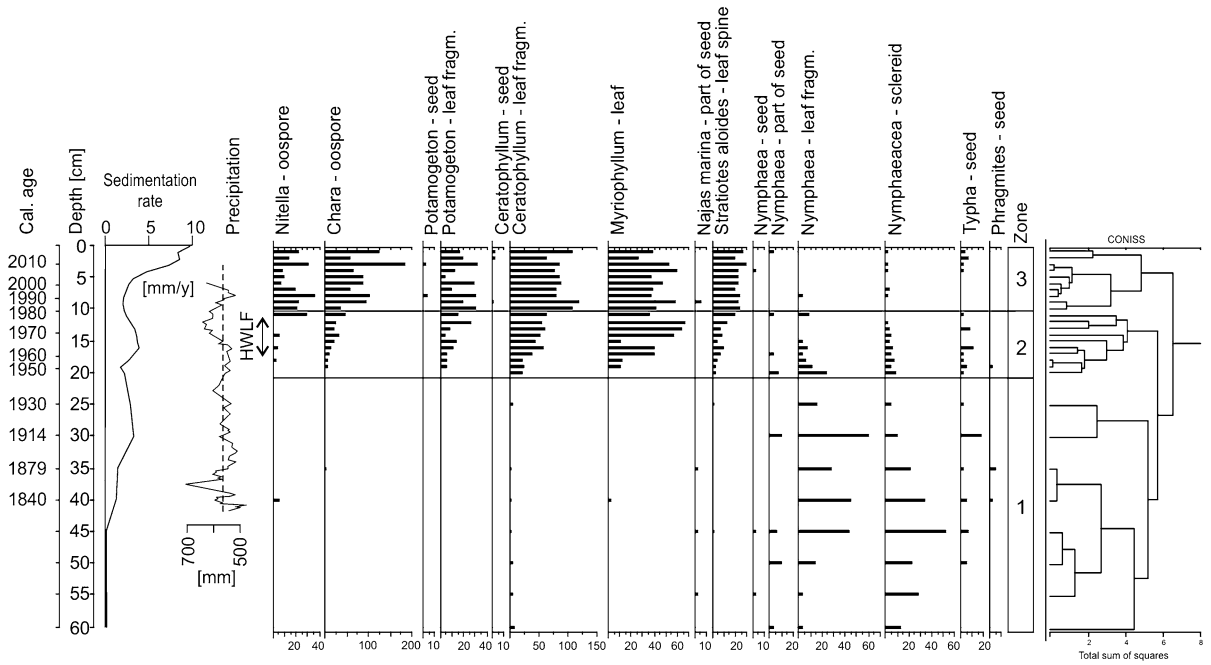

Fig. 3 Concentrations of plant macrofossil remains in the sediment core KL-2, expressed in numbers per 100 cm^3 of fresh sediment. To the *left*, sedimentation rate (mm/year), and precipitation (mm). The latter is based on an 11-year monitoring of the mean annual precipitation for Warsaw; the *hatched line* shows the mean value for the observation period (after Przybylak, 2010). HWLF—period of extensive hydrotechnical works in the catchment and High Water Level Fluctuations

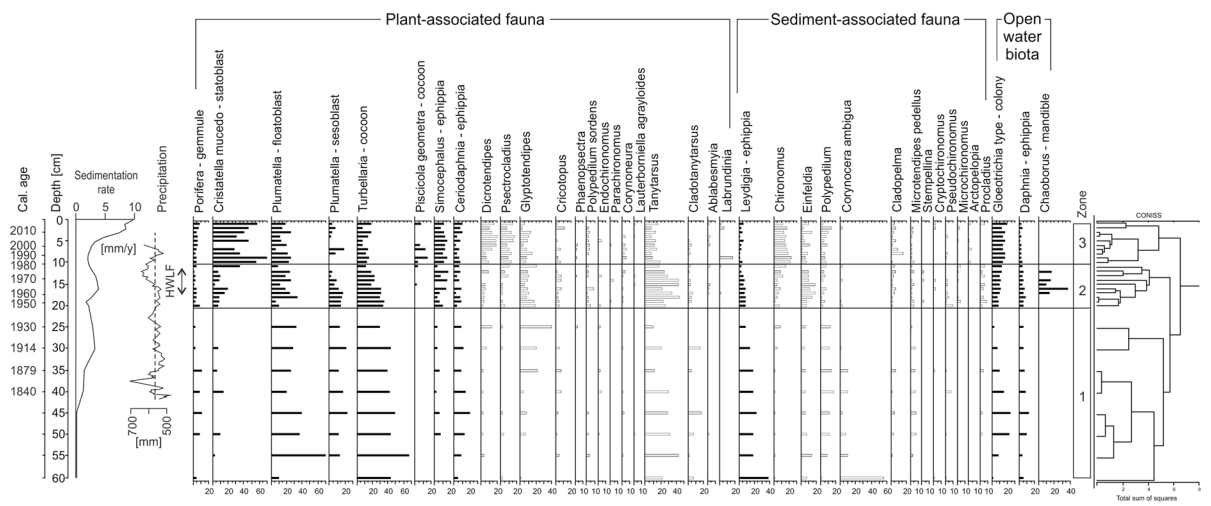

Fig. 4 Concentrations of invertebrate and *Gloeotrichia* macrofossil remains, expressed in numbers per 100 cm^3 of fresh sediment (*black bars*), and percentages of Chironomidae (*white bars*) in the sediment core KL-2. To the *left*, sedimentation rate (mm/year), and precipitation (mm). For explanations concerning precipitation and HWLF abbreviation see Fig. 3

decreased in diversity, and remained in regress. There was a prevalence of *Chironomus* sp. and *Polypedilum* sp. *Cladopelma* sp., present in all of the layers, was still relatively numerous.

Discussion

Reconstruction of the lake history

Throughout the sediment record, Lake Kleszczów was probably surrounded by an emergent belt composed of *Typha* sp. and *Phragmites* sp., as suggested by their seeds preserved in the sediments (Fig. 3). The macrophytes deposited in the earliest (60–55 cm, pre-1840) period were about equally composed of submerged *Ceratophyllum* sp. and floating-leaved *Nymphaea* sp., both typical of habitats with abundant nutrients (Egertson et al., 2004; Penning et al., 2008). Nymphaeids increased significantly in the next core section (55–40 cm), suggesting a lake dominated by floating-leaved vegetation. A relatively strong development of the nymphaeid zone could have been related to a low water level (probably lower than the current lake level by 1–1.5 m). Abundant Nymphaeids would have shaded the water column and thereby reduced the development of both phytoplankton and submerged vegetation. Nymphaeid leaves, both floating and submerged, can also act as effective refuge for filtering planktonic crustaceans, which control the development of phytoplankton (Timms & Moss, 1984; Moss et al., 1998). At low water levels, fish-kills were likely to occur, especially during hot summer days, triggering a cascading effect, resulting in a reduction in phytoplankton biomass (Carpenter et al., 1985; Moss et al., 1998). Therefore there is some reason to believe that the ecosystem at this time remained in the clear-water state.

Submerged vegetation, being shaded by floating leaves of nymphaeids was probably poorly developed. It was continuously represented by *Ceratophyllum* sp., and by periodically occurring *Najas marina* and *Myriophyllum* sp. In contrast to planktonic producers, they can use the phosphorus resources deposited in sediments (Carpenter & Lodge, 1986; Moss, 1998a; Marion & Paillisson, 2003; Brenner et al., 2006). Phytoplankton is generally dependent on the concentration of nutrients in water (Moss, 1998a; Scheffer, 1998). An exception in Lake Kleszczów was the colonial *Gloeotrichia echinulata*, which was numerous, particularly between 55 and 40 cm. It is a large (1–3 mm diameter) cyanobacterium typical of nutrient-poor lakes. Its overwintering resting cells absorb substantial amounts of phosphate from the sediment pore water during germination, before recruitment into the water column (Carey et al., 2008; Carey & Rengefors, 2010). In this way, the activity of *G. echinulata* may, over time, result in a transfer of nutrients from the sediments back to the water column.

Submerged vegetation did not generally develop large dense patches. Considerable areas of the bottom must have been devoid of vegetation, as suggested by numerously occurring, at least in the initial period, chironomid *Corynocera ambiqua*, requiring exposed soft sediments, with a preference for a bottom overgrown by charophytes (Brodersen & Lindegaard, 1999). Similar conclusions can be drawn based on the presence of the cladoceran *Leydigia* sp., also showing a preference, connected with its feeding mode, for sediment surfaces (Dodson & Frey, 2001; Rybak & Błędzki, 2010).

In core section 40–22 cm, covering a period probably of ca. 100 years (~1840–1940), the mean sedimentation rate was much higher than in the previous period and fluctuated between 1.3 and 3.3 mm/year (Fig. 3). Although affected by diagenesis and sediment compaction, this may reflect a gradual increase in productivity, reflected in increased hydrophyte production, from human impacts intensifying at the time. An increase in trophic status is consistent with an increase in the percentage of *Glyptotendipes*, a chironomid preferring nutrient-enriched waters (Kornijów & Gulati, 1992; Brodersen & Quinlan, 2006; Tarkowska-Kukuryk & Kornijów, 2008), and a simultaneous decrease in the numbers of colonial cyanobacteria *G. echinulata*.

Despite the increase in productivity, the nymphaeids that strongly developed in the earlier period gradually regressed. The cause could be a significant increase in the water level in the years 1830–1855 owing to rain about 40% higher than today (Przybylak, 2010). A few years later there was a long period of severe drought (1863–1889; Fal, 2004), which could lead to lower water levels and thus to improved conditions for the nymphaeids. However, low rainfall was accompanied by a decade (1865–1875) of very severe winters and thus thick and long lasting ice cover (Piotrowicz, 2010). This could, together with a thick

snow cover, have a destructive impact on macrophytes, which has been reported in several cases (Renman, 1989; Rintanen, 1996; Caisova & Gąbka, 2009). Scheffer et al. (2003) also underline the high sensitivity of floating-leaved plants to harvesting/mechanical damage. The entire period of about 100 years can thus be viewed as unfavourable for the development of nymphaeids. Similar conclusions were drawn by Kowalewski et al. (2013), reconstructing the history of the development of vegetation at nearby Lake Głębokie Uścimowskie.

Starting from 40 cm a gradual decline in growth of nymphaeids was accompanied by a continuous presence of submerged angiosperms, and periodically appearing charophyte clusters. Turbellaria and the bryozoan *Plumatella* sp. developed abundantly. Porifera and the bryozoan *Cristatella mucedo,* which are indifferent to the lake trophic level (Økland & Økland, 2000) were less abundant. The decreasing abundance of *Corynocera ambiqua* and *Leydigia* sp. suggests an increase in the bottom area occupied by macrophytes, offering a shelter against predators for phytophilous crustaceans such as *Ceriodaphnia* sp. and *Simocephalus* sp. (Adamczuk, 2010; Rybak & Błędzki, 2010). The free water zone among the vegetation patches, could be potentially inhabited by pelagic *Daphnia* sp.

In the first decade of the twentieth century (~30 cm), drainage works began in the vicinity of the lake. The sedimentation rate reached its first highest value at that time. One consequence of drainage works could have been periodic recession of submerged plants, as suggested by the lack of their remains in the sediment. The high abundances of *Typha* sp. seeds suggest a reduced water level, and expansion of the emergent reed swamps (Egertson et al., 2004). A reduced water level is also suggested by the numerous remains of nymphaeids.

In Figs. 3 and 4, zone 20–11 cm, corresponding to the years 1947–1987, is clearly distinguished. At first, the sedimentation rate decreased again to a range of 1.7–2.7 mm/year. This could have resulted from reduced human pressure from the slowing down of economic development and farming intensification during World War II. Another notable feature during this period was a prolonged drought over a large area of eastern and middle Poland, including the drainage basin of the River Wieprz, between 1947 and 1954 (Fal, 2004; Janicki et al., 2011), which led to very low water flows in the River Tyśmienica (Michalczyk & Sobolewski, 2009) whose catchment area includes Lake Kleszczów. The drought probably contributed to the depletion of the groundwater table, continued drawdown of the lake and a decrease in the maximum depth to 2.3 m in 1950 (Wilgat, 1954), which was 1.6 m less than the estimated depth in 1839 and 0.7 m less than today. The drawdown appeared to trigger the colonisation of almost the entire central part of the lake by submerged vegetation, with large patches of charophytes in the eastern part of the lake basin. This was confirmed by the first limnological analyses conducted in the lake. According to Wilgat (1954), in 1950, the lake bottom was covered with a "dense underwater meadow". More detailed data are provided by Fijałkowski (1959) who studied the lake flora between 1953 and 1957 and described Lake Kleszczów as "the lake richest in macrophytes" in the region. The plant community in the central part of the lake was dominated by *Ceratophyllum* sp., *Chara globularis*, *Elodea canadensis and Stratiotes aloides* were particularly abundant along the shores (Fig. 1). These are plants without, or with only weakly developed roots. Together with periphyton, they primarily absorb nutrients from the water column, and integrate them into their biomass, leading to a decrease in the habitat's productivity (Jeppesen, 1998). The lake's trophic status indeed seemed to be decreasing, as suggested by a decrease in *Glyptotendipes* sp. and an increase of fossils of *C. mucedo*, *G. echinulata*, all of the eutrophication-sensitive species.

The situation has been changing since 1960s, the beginning of extensive use of mineral fertilisers, as well as extensive hydrotechnical works. These measures resulted in the lake becoming a storage reservoir, subject to considerable water level fluctuations. This is concordant with a decreased abundance of remains of Bryozoa (Fig. 4), as a response to an increase in siltation (Okamura, 1997) and periodic drying out and freezing of the emergent plants. The maximum depth of the lake during summer 1968 was only 1.5 m (Popiołek, 1971), one meter less than in 1950 (Wilgat, 1954), and less than half of today's level. This could have facilitated sediment resuspension, which would also have been favoured by the reduced vegetation cover (Blindow et al., 2014, Jeppesen et al., 2015). Organic matter from the exposed lake shore, and humic acids leached from the adjacent peat bogs, could have contributed to an increased concentration

of dissolved and suspended matter in the water, as suggested by periodically exceptionally low transparency, amounting to 1 m (Kowalczyk, 1979). This might account for the considerable increase in the sedimentation rate, averaging around 3–4 mm/year (Figs. 3 and 4). At approximately the same time, the development of *Procladius* sp. also increased, as a characteristic response of this midge to rapid changes in sediment deposition (Warwick, 1980; Little & Smol, 2000; Langdon et al., 2006).

Information on the composition and distribution of vegetation in the lake is supplemented by Popiołek (1971) who conducted botanical research in 1968–1969. The near-shore zone was occupied by patches of *Myriophyllum spicatum*, resistant to water drawdown and preferring nutrient-rich waters (Penning et al., 2008; Sondergaard et al., 2010) (Fig. 1). The central part of the lake was colonised by the *Stratiotes aloides* community. *S. aloides*, considered to prefer highly hydrated and loosely packed organic sediments (Kłosowski et al., 2011), and to be a fast coloniser of shallow water bodies (Smolders et al., 1995; Królikowska, 1997; Sugier et al., 2010), provides a specialised habitat for accompanying organisms. Its ecological characteristics have been discussed in several papers (Higler, 1977; Kufel et al., 2007; Strzałek & Koperski, 2009). Unlike the majority of other freshwater angiosperms (Newman, 1991), it is susceptible to herbivory, particularly by leaf-mining insect larvae (Higler, 1977; Linhart, 1999; Tarkowska-Kukuryk, 2006). The extensive meadows of charophytes reported by Fijałkowski in the 1950s were virtually absent. Their disappearance may have been caused by the thick and long-lasting (exceeding 120 days) ice cover during a series of exceptionally severe winters in the years 1962–1964, 1968–1970 and 1995/1996, the coldest in the second half of the twentieth century (Skowron, 2003). Alternatively, the temporary disappearance of charophytes could have been caused by increased water level fluctuations, and the related increased turbidity. It is very likely that both of the factors, hydrological disturbances and ice cover, acted together. Only small patches of charophytes remained among the *M. spicatum* meadows (Fig. 1). They were formed, however, not by *C. globularis* as in the 1950s, but by *C. vulgaris,* a species tolerant of water level fluctuations (Van Geest et al., 2005) and of turbid and nutrient-rich conditions (Van den Berg et al., 1997; Van den Berg & Coops, 1999). Increased abundance of *Typha* sp. seeds in the sediments suggests widening of the reed-swamp zone.

Only during that period, affected by hydrotechnical works, did the mandibles of predatory larvae of *Chaoborus* (most probably common in the area *C. flavicans* Guignot; Kornijów, unpubl.) appeared and occurred in high percentages. Their coexistence with fish requires low water clarity (Wissel et al., 2003; Tolonen et al., 2012). The appearance of *Chaoborus* sp. larvae could have also been related to a generally reduced feeding pressure by fish. The considerably decreased water level and exceptionally long-lasting ice cover in the years 1962–1970 could have easily induced winter fish-kills and release of planktonic crustaceans from predation pressure. This, in consequence, would also have resulted in increased top-down effects of grazing on phytoplankton (Jeppesen, 1998). The fish-kills are short-term events, however, and not easily detectable with the coarse resolution of the sediment record (Amsinck et al., 2005).

The last stage of the lake's history (10–1 cm), from the end of 1980s to the present, is a period with no major hydrological disruptions. The continued development of submerged vegetation, and particularly charophytes, progressed (Fig. 3). An increase in the abundance of *G. echinulata* suggests a low level of phosphorus in the water column, though the limited chemical data shows values around the mean for the last half-century. The fossil plant-associated fauna are very taxa rich and abundant (Fig. 4). From only this period, numerous cocoons of fish leech *Piscicola geometra* were found. They are proposed as a simple palaeolimnological indicator of the presence of submerged macrophytes in lakes (Odgaard & Rasmussen, 2001; Sayer et al., 2010a). The sediments were particularly rich in larvae of *Chironomus* sp. They are capable of enduring periodical oxygen depletion at the water/sediment interface (Walshe, 1950; Brodersen & Quinlan, 2006), potentially reflecting the accumulation of organic matter and strongly damped water movements under densely growing charophyte meadows (Van den Berg et al., 1997; Miranda & Hodges, 2000; Madsen et al., 2001).

The information recorded in the sediments is supplemented by contemporary observations. Sugier and Czarnecka (1998) noted that in 1995 almost the entire surface was overgrown by submerged vegetation dominated by *C. vulgaris* (Fig. 1). It was probably prevalent for ca. 15 years, until the end of the 1990s.

In 2000–2001, the continued dense growth of charophytes was dominated by *C. globularis* while *C. vulgaris* diminished, as it did in the 1950s (Lorens & Sugier, 2001). With slight changes, the charophyte communities have been maintained until 2014. *C. globularis* continues its dominance but *C. delicatula* plays an increasingly important role. It is a species preferring less productive waters than *C. globularis* (Pełechaty et al., 2004), and its development may suggest a progressive oligotrophication of the environment. This coincides with a reduction in fertiliser use in the catchment during this period.

Implications for the concept of alternative regimes

Both paleolimnological records and recent limnological studies show that Lake Kleszczów has not experienced a phytoplankton-dominated state in its recent history of several 100 years. Thus our hypothesis that the current macrophyte-dominated state of the lake has been a persistent feature over the recent centuries cannot be rejected. This seems to be typical of lakes in a landscape generally unaffected by human activity (Moss, 1998a; Scheffer, 1998; Little & Smol, 2000; Davidson et al., 2005; Salgado et al., 2010, Kowalewski et al., 2016).

For centuries, Lake Kleszczów was dominated by floating-leaved vegetation, probably in a situation of strongly reduced water level. Submerged macrophytes, poorly developed in the lake due to shading by nymphaeids were represented predominantly by angiosperms and, in particular, by *Ceratophyllum* sp. The gradual regression of nymphaeids started in the mid-19th century, probably as a result of climate fluctuations that at first were responsible for the strong increase, and then lowering of the water level and for plant freezing. Elodeids developed abundantly in the mid-twentieth century. Since then there was dominance by submerged macrophytes, mostly *Ceratophyllum demersum* and *Myriophyllum spicatum*.

Only in the second half of twentieth century was there a shift towards charophytes. The drainage in the 1960s was sufficient to return the lake to a state dominated by floating *Stratiotes aloides* for several years. It was not a typical dominance state, as described as floating-plant dominance (Scheffer et al., 2003), with shaded and deoxygenated water under floating carpets of vegetation (e.g., Kornijów et al., 2010, 2016) and nutrient release from the sediments (Pinto & O'Farrell, 2014). Below the floating carpet of *S. aloides*, evergreen submerged macrophytes occurred (*Elodea canadensis* and *C. demersum*). In the long term, *S. aloides* does not tolerate water level fluctuations (Otahelová & Banasová, 1997), which occurred during the further management of the lake as a retention reservoir. A strong decline of the plant in the following years (Sugier & Czarnecka, 1998) can be therefore attributed to hydrological stress. Before that, however, together with the remaining angiosperms, the plant could have contributed to restriction of phytoplankton development, and an increase in water clarity, owing to competition for nutrients, allelochemical effects (Kufel et al., 2007) and provision of an efficient daytime refuge for filter-feeding Crustaceans (Strzałek & Koperski, 2009). The improved light climate, and possibly also decreased nutrient availability (Sondergaard et al., 2010; Hilt et al., 2013; Blindow et al., 2014) could have permitted the colonisation of the lake bottom by charophytes, starting with *Chara vulgaris,* resistant to water level fluctuations and stranding at the lake edges. Its several patches among watermilfoil meadows were recorded in 1968 (Fig. 1). They must have expanded gradually. In the mid 1990s, they covered almost the entire lake with dense carpets. Charophytes were then dominated by *C. vulgaris*, but *C. globularis* had already appeared among them. In the following stages of succession, at the turn of the 21st century, there was dominance by *C. globularis*, with a gradually increasing contribution of *C. delicatula*. Our research supports the finding reported from periodically flooded oxbow lakes (Van Geest et al., 2005), where charophyte beds responded to increased water level fluctuations by changes in balance between *C. vulgaris,* resistant to hydrological disturbances and non-resistant *C. globularis*. We suggest that this pattern may serve as a useful tool for determining periods of substantial changes in water level.

During the last few 100 years Lake Kleszczów was periodically dominated by three types of vegetation: floating-leaved plants, submerged angiosperms and charophytes (Fig. 5). The transition from one type of vegetation to the other was induced by changes in productivity and water level, as a consequence of both natural (weather) and anthropogenic (drainage and water-level management) processes. An important role was likely played by a periodic cooling of the

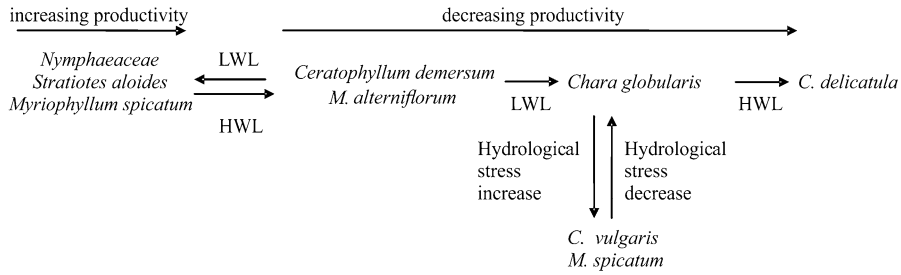

Fig. 5 Conceptual model of changes in floating-leaved and submerged macrophyte communities in the shallow Lake Kleszczów, as a response to alterations in productivity and hydrology. *LWL* low water level, *HWL* high water level

climate, leading, especially at low water, to the destruction of vegetation.

During the last 60 years the lake has remained in a clear-water state, first dominated by *C. globularis*, followed by *Stratiotes aloides*, *C. vulgaris*, and again by *C. globularis.* The year-round persistence of the submerged vegetation must have been of high importance for the lake with retention of nutrients in the plant biomass, even in winter, restricting the development of phytoplankton (Scheffer, 1998). Moreover, the continuous presence of macrophytes reduces the risk of e.g., cold conditions delaying the growth of submerged macrophytes in early spring, which could favour algal development (Blindow et al., 1993; Bayley et al., 2007; Sayer et al., 2010b; Hilt et al., 2013). Year-round vegetation provides rich resources of epiphytic fauna as food for fish, reducing their pressure on zooplankton (Diehl & Kornijów, 1998; Kornijów et al., 2005, 2016). It simultaneously restricts the access of benthivorous fish to bottom sediments, and the possibility of bioturbation and resuspension (Moss, 1998b; Scheffer, 1998). It also provides refuges for filter-feeders against predators. This strengthens the potential top-down effect (Jeppesen, 1998) resulting from a high contribution of piscivorous fish in the total biomass of fish. In Lake Kleszczów, the ratio of predatory/nonpredatory fish was very high (almost 1:1), whereas the zooplankton/phytoplankton ratio amounted to 12.4 (Kornijów et al., 2002).

Blindow et al. (2014) question the role of charophytes as shelter places for zooplankton, because Cladocera biomass in charophyte lakes can be low. The same authors explain this seeming contradiction with very low development of phytoplankton owing to a shortage of nutrients, permanently integrated into the biomass of charophytes. This suggests a role for bottom-up mechanisms for the maintenance of the clear-water state in charophyte lakes that is greater than that of top-down mechanisms.

The year-round coverage of sediments by dense charophyte beds, however, can have long-term consequences, including an increase in "internal eutrophication". The reduction of P concentration in the water column is accompanied by the accumulation of P in lake sediments originating from dead plant and animal remains, and enhanced by co-precipitation with the charophytes' calcite encrustations (Carpenter, 1981; Kufel & Kufel, 2002). On the one hand, this limits phytoplankton production and provides clear-water for macrophyte growth. On the other, it increases sediment oxygen demand causing anaerobic conditions that can boost P release from the anoxic sediment and fertilisation of water column. This might lead to lower resilience of the current clear-water state, and an increased probability of a shift to phytoplankton dominance and turbid water. This mechanism is suggested to be a trigger behind a repeated pattern of shifts between clear and turbid states (Rip et al., 2005; Hargeby et al., 2007; van Nes et al., 2007; Randsalu-Wendrup et al., 2014). In Lake Kleszczów, no such cyclic shifts were recorded despite a relatively wide range of TP concentrations (19-60 $\mu g\ l^{-1}$) over more than 40 years (Table 1). The chemistry data is insufficient to reveal any pattern in TP fluctuations.

The range of TP where lakes are most likely to switch from one state to another in a temperate climate is between 25 $\mu g\ l^{-1}$ and 100 $\mu g\ l^{-1}$ (Scheffer & Jeppesen, 1998; Moss, 2007b). In lakes where submerged plants cover almost the entire bottom surface, however, as is the case for Lake Kleszczów, it may be several times higher (Bayley et al., 2007). The

threshold value is influenced not only by the vegetation cover, its composition, and seasonal dynamics of biomass, but also by the structure of ichthyofauna and contribution of planktivorous and piscivorous fish to the strength of top–down interactions. This involves various relationships, both trophic, among phytoplankton, periphyton, macrophytes, invertebrates, fish and waterfowl, and paratrophic, resulting from the habitat structural complexity or allelopathic interactions (Moss et al., 1996; Moss, 1998a; Scheffer, 1998). Therefore, thresholds with respect to any particular variable are often functions of other factors. Simplified models also suggest that such shifts can occur in relatively rare cases (van Nes et al., 2007).

Another approach to the mechanisms of transition from the macrophyte-dominated state to turbid water state with the dominant role of phytoplankton is presented by Moss (2007a, b). He believes that an external driver is needed to make the switch. The nutrients are not the driver themselves, but they influence the threshold for the real driver (which might be a whole range of things from mechanical damage to the plants, herbicides or intense bird grazing, boat damage, violent storms or biocides affecting zooplankton or periphyton grazers). Such an approach calls into question the possibility of a spontaneous shift towards a turbid state resulting from internal eutrophication.

Our study provides support for this idea. It shows that within a longer period of clear water and abundant submerged or floating-leaved vegetation, the community of macro-vegetation can be dynamic, because dominance patterns change as a response to different productivity level and/or hydrological stress. Therefore, the macrophyte-dominated state defined in general terms, sustaining the clear water phase, can be represented by various types of vegetation, largely determining the composition of other hydrobionts and course of various processes, and as a consequence, the functioning of the ecosystem and its resilience.

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Compliance with ethical standards

Conflict of interest None of the authors has conflict interests, financial or otherwise.

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